A REVIEW OF THE NESTING BEHAVIOR AND OBSERVATIONS ON *TACHYPHEX POMPILIFORMIS* IN NORTH AMERICA (HYMENOPTERA: SPHECIDAE)[1]

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ABSTRACT: Observations on the nesting behavior of Nearctic populations of *Tachysphex pompiliformis* are summarized. A previous study of *T. tenuipunctus* (=*T. pompiliformis*) is scrutinized in order to ascertain the species of *Tachysphex* observed. Observations on the nesting behavior of females of *T. pompiliformis* from the Upper Peninsula of Michigan and upstate New York are given. The wasps nested in sandy or gravelly soil, excavated burrows with the mandibles and forelegs, left entrances open during hunting and provisioning, transported prey on the ground, using the wings as an aid, and filled burrows with sand, using the forelegs and end of abdomen. The single-celled nests were short, shallow, and oriented obliquely. Cell provisions consisted of a single *Melanoplus* sp. (Acrididae) placed head inward and ventral side up. The wasp's egg was affixed to the prey's forecoxal corium and extended transversely across the sterna between the fore- and midcoxae. Behavioral similarities and differences between *T. pompiliformis* and related species are discussed.

Tachysphex pompiliformis (Panzer) has gone unrecognized in North America until recently, despite the fact that it is one of the most commonly collected species in the genus (Pulawski 1988). This species is widely distributed, occurring throughout the cooler parts of the Nearctic and Palearctic faunal zones (Pulawski 1971, 1988), e.g., mountain ranges in the western United States. Its behavior has been studied for nearly a century in Europe (summary in Pulawski 1971), but accounts of its nesting vary widely between studies. In the Nearctic region, only a moderate amount of biological information is available for *T. pompiliformis,* and some of these earlier observations may pertain to other species.

Previous Observations in North America

Peckham and Peckham (1905) were the first to study this species in North America (under the name *T. quebecensis*). They observed a female in July near Milwaukee, Wisconsin that exited from her nest, left the entrance open and flew away. An hour later she came "leaping along," holding a small grasshopper with the third pair of legs. She placed the prey

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in the entrance, turned around inside the nest, pulled in the grasshopper and then exited. In 30 min she added two more prey to the nest and closed it from within. They gave no information on the structure of the wasp's nest or its dimensions, but indicated that the wasp's egg had been placed in front of the first pair of legs of the grasshopper.

Newton (1956) reported on *T. pompiliformis* (as *T. tenuipuncius*) and what he thought were 10 unnamed species of *Tachysphex* nesting in an aggregation near Shoshone, Idaho. Seven of the unnamed species have since been identified by Pulawski (1988) as *T. montanus* (Cresson), *T. eldoradensis* Rohwer, *T. hopi* Pulawski, *T. williamsi* R. Bohart, *T. occidentalis* Pulawski, *T. yolo* Pulawski, and *T. tarsatus* (Say) and, although some of Newton's (1956) observations probably pertain to *T. pompiliformis,* they may refer as well to any of these species. Newton noted that the wasps he studied ranged in body length from 10-16 mm, with a mean of 13 mm. However, *T. pompiliformis* females are only 7-11 mm in body length with a mean of about 9 mm (Pulawski 1988). Figures in Newton's paper show a female of a *Tachysphex* sp. excavating a burrow and the same or another wasp transporting prey on the ground. Both photographs show a wasp with a black head and thorax and red abdomen. Based on size range and coloration, *T. montanus, T. pompiliformis,* or, possibly, *T. amplus* may have been the species Newton observed. Like *T. pompiliformis, T. montanus* is an inhabitant of montane regions in the western United States. Females are 11-14 mm in body length and many of them have an all red abdomen (Pulawski 1988). There are females of *T. montanus,* as well as those of *T. pompiliformis,* pinned with prey from Newton's study in the U.S. National Museum. *T. amplus* has been collected in similar habitats in Idaho. The females are 11-13 mm in body length, and the gaster is all red (Pulawski 1988). All of the *Tachysphex* species named above appear to have similar nesting behavior (Kurczewski 1987, Pulawski 1988).

The wasps Newton observed left their nest entrances open after excavation, straddled the prey venter-up, held it by its antennae, transported it on the ground, often aided by buzzing the wings, and then pulled it into the nest. After immobilizing the prey, wasps were seen to malaxate the sternal area of the grasshopper and imbibe fluids that became disgorged from the mouth. After oviposition the wasp filled her burrow and then excavated a second burrow "within a few inches" of the first one. The population of wasps he observed exhibited an unusually brief time of 3 to 8 minutes to excavate the nest.

The nests entered the soil diagonally and were "1-1/2 to 2 inches deep." During early June each cell was provisioned with two "small" acridids, but later in the summer the wasps stored only one "larger" acridid

per cell. The females preyed nearly exclusively on nymphal *Oedaleonotus enigma* (Scudder), but twice captured nymphs of *Aulocara elliotti* (Thomas), and once, nymphal *Melanoplus* sp. (all Acrididae). The wasp's egg was 2 mm long, affixed to the forecoxal corium, extended transversely across the sterna, and hatched in 2-3 days.

Alcock (1973) studied three nests of *T. pompiliformis* (as *T. parvulus)* in late July at Seattle, Washington. All three nests had been dug into the slope of a path in dense vegetation. They were 1-celled, 5.5-10.0 cm ($\bar{x}$=7.2) long, and 2.5-3.5 cm ($\bar{x}$=3.0) deep. Two fully provisioned cells each held two acridids, 11 mm long, and a third, unfinished cell contained a single large grasshopper 21 mm long. All prey were positioned venter-up, and the wasp's egg had been affixed to the venter of the prothorax of the second prey brought into the first two nests.

Steiner (1981) noted that the prey of *T. pompiliformis* (as *Tachysphex* sp.) was paralyzed by a series of four successive stings. He described the sites of sting insertion, three near the leg bases and one in the throat region. Krombein (1967) listed two genera of immature Acrididae as prey of this species (as *T. quebecensis*) and Pulawski (1988) listed two genera of nymphal acridids as *T. pompiliformis* prey.

Our Observations

Our study of nesting behavior in this species comprised sporadic observations made on eight wasps at five localities in the Upper Peninsula of Michigan and upstate New York. One wasp (Ethology note no. P86-15) nested on 27 June 1986 at 1735 h (EDT) in moss-covered sand at the edge of a trail leading through an old field at the Huron Mountain Club, Marquette Co., MI; three (MFO 9-11) in a 1 m2 area of sand surrounded by grasses and mixed coniferous-hardwood woodlands at 1200-1215 h (EDT) on 10 June 1978 near Parishville, St. Lawrence Co., NY; one (TX-92) at the edge of a field adjacent to a gravel bank on 13 June 1967 in Groton, Tompkins Co., NY; two (TX-90a,b) on 8, 18 June 1968 in a sandy field at the edge of a stand of *Pinus strobus* near Chittenango, Madison Co., NY; and one (TX-91) on 12 June 1971 along a car path leading through a sandy field inside Selkirk Shores State Park, Oswego Co., NY. Observations were made on sunny days at ambient temperatures of 18° - 28°C.

Burrow excavation was observed once. The wasp used her mandibles and forelegs in unison to remove sand from the burrow. She held her antennae outstretched but lowered toward the sand and held her wings flat on the dorsum. Periodically, she backed from her excavation to remove sand that had accumulated inside of the burrow entrance. As she dug deeper, it took her longer to back out with a load of sand. Eventually, the wasp appeared headfirst inside of the entrance, walked onto the tumulus,

ran around the opening three times and went off hunting. The time expended for burrow excavation was 16 min. No leveling of the tumulus was noted. Two other tumuli were 17 x 25 and 25 x 30 mm wide and long, respectively.

Females hunted for prey on the ground and low vegetation, often within 10 m of their nests. They alternated between running and making short, rapid flights between clumps of prostrate vegetation. Prey capture was not observed. Malaxation was seen twice. It involved the wasp squeezing the area of the prey's forecoxal corium with the mandibles, and possibly, lapping up a fluid in the process. During prey transport the wasp straddled the grasshopper venter-up, grasped its antennae with the mandibles and its body with the hindlegs, and proceeded rapidly forward on the ground, using the wings to aid momentum. The head of the paralyzed acridid was placed inside the entrance while the female entered the burrow, turned around within, appeared headfirst in the entrance, and backed inside, holding the prey's antennae with the mandibles. Wasps then appeared headfirst, 2.5 - 5.0 min. after entry and began filling the burrow with sand. The female came onto the surface and flung sand backward with the forelegs, backed inside the burrow while raking sand, and packed the fill into the tunnel with the vibrating end of the abdomen. Two such closures took 6 and 8 min.

The burrows entered the sand obliquely at 45° angles or less to the surface and ended in single cells. Entrances were 6-7 mm ($\bar{x}$=6.7, n=4) and burrows, 4.5-6.0 mm ($\bar{x}$=5.5, n=4) in diameter. Burrows were 24-50 mm ($\bar{x}$=40.4, n=8) long, including cell length, and 15-22 mm ($\bar{x}$=20.8, n=8) deep, including cell depth. Cell sizes ranged from 6-9 mm ($\bar{x}$=8.1, n=8) wide and 12-18 mm ($\bar{x}$=15.7, n=8) long. Each cell contained a single, relatively large (12.5-17.5 mm long) prey placed head inward and ventral side up. The wasp's egg was attached to a forecoxal corium of the prey and extended transversely between the bases of the fore- and midcoxae. The prey were identified as four nymphal *Melanoplus* sp. (MFO 9-11, P86-15); one adult male *M. viridipes eurycerus* Hebard (TX-92); one *M.* sp., possibly *bivittatus* (Say) (TX-91); and two *M.* sp., probably *sanguinipes* (F.) (TX-90a,b) (all Acrididae). Four females of *T. pompiliformis* in the U.S. National Museum are pinned with nymphal acridids as follows: *Melanoplus* sp., 13.5 and 14.0 mm long; *Oedaleonotus enigma,* 12.5 mm long (2) (Table 1).

DISCUSSION

No fewer than 19 European workers have studied the nesting behavior of *T. pompiliformis*, often as its synonym, *T. pectinipes* (L.). Morphologically and ecologically, *T. pompiliformis* is a variable species. The number of generations per year varies from one in northern Europe (Pulawski 1971)

to two in Italy (Bonelli 1966). The most confusing aspects of its nesting, based upon these studies, involve whether or not the wasp appropriates pre-existing cavities for nesting sites, the exact method of prey transport, number of cells per nest, and number of prey per cell. Both Maneval (1932) and Crevecoeur (1951) have noted that females frequently renovate a subterranean cavity for a nest, yet many other workers have reported that the nest is excavated from the ground surface. Bonelli (1966) and Pulawski (1971) each reported that the prey is straddled dorsum-up, yet other workers noted transport of prey in a venter-up position. Most workers have recorded single-celled nests of *T. pompiliformis,* yet Adlerz (1904) noted three-celled nests of this species in Sweden. Many workers, notably Bonelli (1966), have recorded one, two, or three paralyzed acridids per cell; however, Maneval (1932) listed one large and 6 to 10 small prey per cell. Large grasshoppers were carried on the ground and small ones, in flight. Hardouin (1938) questioned the validity of Chevalier's (1924) observation of seven prey in one cell of *T. pompiliformis* and, therefore, would have probably also been skeptical of Maneval's (1932) report of 6-10 prey per cell for this species. The discrepancy in reports on the nesting behavior of *T. pompiliformis* in Europe is difficult to clarify because many of the observations are ambiguous or sketchy, at best, and some appear to involve doubtful identification of the wasp species.

The behavioral reports on the Nearctic populations of *T. pompiliformis*

Table 1. Genera and species of prey Acrididae of *Tachysphex pompiliformis* in North America.

Genera and species of prey*	Source of information
Aulocara elliotti (Thomas)	Newton 1956, Pulawski 1988
Camnula pellucida (Scudder)	Kurczewski 1964, Krombein 1967
Melanoplus viridipes eurycerus Hebard, Adult	FEK TX-92
Melanoplus sp., possibly *bivittatus* (Say)	FEK TX-91
Melanoplus sp., probably *sanguinipes* (F.)	FEK TX-90 a, b
Melanoplus spp.	Newton 1956, Kurczewski 1964, Krombein 1967, Pulawski 1988, MFO 9-11, P86-15
Oedaleonotus enigma (Scudder)	Newton 1956

*Nymphs unless indicated otherwise.

which have been published under the names *T. quebecensis* (Peckham and Peckham 1905), *T. tenuipunctus* (Newton 1956) and *T. parvulus* (Alcock 1973) are easier to interpret. Despite the fact that these studies were made at widely separated locations, there is some agreement on the details of nesting behavior. Newton's (1956) observations, although excellent, can be questioned because of the doubtful identity of the species of wasp. Our behavioral descriptions for this species conform in many essential elements to these earlier reports.

All wasps nested in early summer (June, July) in sandy or gravelly soil containing moderate amounts of vegetation. Females excavated their burrows, beginning from the ground surface. Entrances were left open while hunting and provisioning, and females ran around the opening several times (probably a form of orientation) prior to hunting. Prey transport was on the ground, or possibly in short flights (Peckham and Peckham 1905), the wasp grasping the prey's antennae with the mandibles and its body with the hindlegs. Females used the wings to aid forward progress. Alcock (1973) photographed a female on a plant stem, holding her prey dorsum-up. Newton (1956) photographed a wasp transporting her prey on the ground in a ventral side up position, but this female is clearly not *T. pompiliformis.* One of us (MFO) noted that the prey was transported venter-up, but we could not ascertain the exact method of grasping the acridid. Wasps released the grasshoppers inside their entrances and pulled in the prey from within the nests.

All nests were short, shallow, unicellular, and entered the soil diagonally to the surface. From one to three acridids were placed in a cell and they were positioned head inward and ventral side up. The wasp's egg was affixed to a forecoxal corium and extended transversely across the pro- and mesosterna between the bases of the first two pairs of legs.

Tachysphex pompiliformis is related morphologically to *T. montanus, T. aethiops* (Cresson), *T. acutus* (Patton), and *T. punctifrons* (Fox) (Pulawski 1988). The first three species inhabit pan-boreal zones of North America, extending southward mostly in mountainous regions (Pulawski 1988). *Tachysphex acutus* and *T. punctifrons* are collected uncommonly in the United States and southern Canada east of the Rocky Mountains (Pulawski 1988). Although the five species are unified by morphological similarities, they can be separated from each other behaviorally (Kurczewski 1987). *Tachysphex aethiops, T. punctifrons,* and *T. pompiliformis* (in Europe) dig multicellular nests and have been reported to begin nests from pre-existing soil cavities (Adlerz 1904, Maneval 1932, Crèvecoeur 1951, Evans 1970, 1973, Alcock 1973, Kurczewski 1987, O'Brien 1987). *Tachysphex acutus* excavates rudimentary bicellular nests from the surface in soil with much vegetation (Kurczewski in press). The nest of *T.*

montanus has not been described, but if Newton's (1956) observations pertain to this species, then it is single-celled. *Tachysphex punctifrons* and *T. pompiliformis* in Europe and, possibly, North America transport prey on the ground, straddling the grasshopper dorsal side up (Kurczewski 1987, Pulawski 1971, Alcock 1973), whereas *T. acutus,* and possibly, *T. montanus* carry their prey on the ground in a ventral side up position (Kurczewski in press, Newton 1956). *Tachysphex montanus* and *T. pompiliformis* capture the same species of Acrididae in Idaho, preying on medium-sized and relatively large nymphs of Oedipodinae and Cyrtacanthacridinae (Newton 1956, Krombein 1967, Pulawski 1988). *Tachysphex acutus* and *T. punctifrons* capture relatively large, nymphal or adult (*T. punctifrons*) *Melanoplus* spp. (Cyrtacanthacridinae) (Kurczewski in press, 1987), whereas *T. aethiops* preys only upon nymphal Oedipodinae (Evans 1970, 1973, O'Brien 1987).

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SOCIETY MEETING-MARCH 16, 1988

If Charles Darwin were alive today, he would instantly appreciate the modern problem of insecticide resistance. It is a dramatic example of natural selection in action. The more effective an insecticide is the greater the selective advantage there is for resistant individuals in the target species. While resistance to DDT in house flies and mosquitoes is well known, over 450 examples of insecticide resistance have been documented. Dr. David Marsden of the E.I. duPont Company, who spoke on "Insecticide Resistance Management", cited the striking example of the Diamond-back moth. This moth with a short life cycle is a year round pest of cruciferous crops in Thailand. Over the years this species has developed resistance to every insecticide used to control it. Clearly it is important to develop strategies of management to minimize, delay, or avoid resistance so that insecticides can be used for a longer time in lesser amounts and still achieve control of insect damage to crops.

Dr. Marsden presented his talk to twelve members and two guests in Townsend Hall at the University of Delaware. He described the many factors such as life history, behavior, and biochemistry that contribute to insecticide resistance. In order to design effective management as much as possible must be known about the target species. Dr. Marsden is participating in a collaborative project with the DuPont Company and four other insecticide producers, "The Pyrethroid Efficacy Group." They have jointly undertaken a large scale effort to monitor and minimize insecticide resistance of *Heliothis virescens* (Lepidoptera: Noctuidae), a major pest on cotton in the cotton growing regions of the southern United States. This program uses both laboratory and field monitoring to assess resistance levels so the appropriate methods of insect control can be used to provide acceptable efficacy and reduce potential buildup of resistant populations. These multiple measures of resistance are being used with sophisticated strategies of insecticide application to preserve the long term use of current chemicals used for *Heliothis* control in cotton. The results so far indicate that the efforts to minimize resistance have been successful.

Harold B. White,
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